

Ecohydrological responses of dense canopies to environmental variability:

2. Role of acclimation under elevated CO₂

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Received 1 March 2010; revised 15 July 2010; accepted 27 July 2010; published 11 November 2010.

[1] The ability to accurately predict land-atmosphere exchange of mass, energy, and momentum over the coming century requires the consideration of plant biochemical, ecophysiological, and structural acclimation to modifications of the ambient environment. Amongst the most important environmental changes experienced by terrestrial vegetation over the last century has been the increase in ambient carbon dioxide (CO₂) concentrations, with a projected doubling in CO₂ from preindustrial levels by the middle of this century. This change in atmospheric composition has been demonstrated to significantly alter a variety of leaf and plant properties across a range of species, with the potential to modify land-atmosphere interactions and their associated feedbacks. Free Air Carbon Enrichment (FACE) technology has provided significant insight into the functioning of vegetation in natural conditions under elevated CO₂, but remains limited in its ability to quantify the exchange of CO₂, water vapor, and energy at the canopy scale. This paper addresses the roles of ecophysiological, biochemical, and structural plant acclimation on canopy-scale exchange of CO₂, water vapor, and energy through the application of a multilayer canopy-root-soil model (MLCan) capable of resolving changes induced by elevated CO₂ through the canopy and soil systems. Previous validation of MLCan flux estimates were made for soybean and maize in the companion paper using a record of six growing seasons of eddy covariance data from the Bondville Ameriflux site. Observations of leaf-level photosynthesis, stomatal conductance, and surface temperature collected at the SoyFACE experimental facility in central Illinois provide a basis for examining the ability of MLCan to capture vegetation responses to an enriched CO₂ environment. Simulations of control (370 [ppm]) and elevated (550 [ppm]) CO₂ environments allow for an examination of the vertical variation and canopy-scale responses of vegetation states and fluxes to elevated CO₂. The unique metabolic pathways of the C₃ soybean and C₄ maize produce contrasting modes of response to elevated CO₂ for each crop. To examine the relative roles of direct reduction in stomatal aperture, observed structural augmentation of leaf area, and biochemical down-regulation of Rubisco carboxylation capacity in soybean, a set of simulations were conducted in which one or more of these acclimations are synthetically removed. A 10% increase in canopy leaf area is shown to offset the ecophysiological driven reduction in latent energy flux by 40% on average at midday. Considering all observed acclimations for soybean, average midday *LE* (*H*) were decreased (increased) by 10.5 (18) [W m⁻²]. A lack of direct stimulation of photosynthesis for maize, and no observed structural or biochemical acclimation resulted in decreases (increases) in average midday *LE* (*H*) by 40–50 [W m⁻²]. An examination of canopy-scale responses at a range of CO₂ concentrations projected to be seen over the coming century showed a general continuation in the direction of

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flux responses. Flux responses showed little sensitivity to assumptions of constant versus linear trends in structural and biochemical acclimation magnitudes over the 400–700 [ppm] concentration range examined here.

Citation: Drewry, D. T., P. Kumar, S. Long, C. Bernacchi, X.-Z. Liang, and M. Sivapalan (2010), Ecohydrological responses of dense canopies to environmental variability: 2. Role of acclimation under elevated CO₂, *J. Geophys. Res.*, *115*, G04023, doi:10.1029/2010JG001341.

1. Introduction

[2] Amongst the most important environmental changes is the likely doubling of atmospheric carbon dioxide concentrations (C_a) from preindustrial levels by the middle of the 20th century [Prentice *et al.*, 2001]. This change in atmospheric composition has been demonstrated to significantly alter a variety of leaf and plant properties across a range of species [Sage *et al.*, 1989; Arp, 1991; Sage, 1994; Long *et al.*, 2004; Ainsworth and Long, 2005] with the potential to modify land-atmosphere interactions and their associated feedbacks [Mooney *et al.*, 1987; Woodward, 1998; Wilson *et al.*, 1999; Gottschalck *et al.*, 2001]. This paper seeks to address the roles of ecophysiological, biochemical and structural plant acclimation on canopy-atmosphere exchange of CO₂, water vapor and energy through the application of a multilayer canopy-root-soil model [Drewry *et al.*, 2010] capable of resolving changes induced by elevated CO₂ through the canopy and soil systems.

[3] The most compelling results pertaining to vegetation acclimation response to date have come from Free Air Carbon Enrichment (FACE) experiments [Lewin *et al.*, 1994; Miglietta *et al.*, 2001], which allow for the examination of ecosystem responses to an enriched CO₂ environment in open-air field conditions, circumventing many of the problems associated with enclosure systems [Arp, 1991; Sage, 1994; Long *et al.*, 2006]. A meta-analysis summarizing FACE results for 40 species from 12 FACE sites reported a 28% increase in diurnal carbon assimilation across all species, with the response several factors greater for plants using the C3 photosynthetic pathway, relative to C4 [Ainsworth and Long, 2005]. Increases in CO₂ concentrations above current ambient levels causes an increase in leaf-level C3 assimilation, as CO₂ is a substrate in the photosynthetic carboxylation reaction and a competitive inhibitor of the oxygenation reaction, both catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) located in leaf chloroplasts [Drake *et al.*, 1997]. In contrast, plants utilizing the C4 photosynthetic pathway are expected to have a much smaller response of photosynthetic assimilation (A) to elevated C_a due to the CO₂-concentrating mechanism of C4 bundle sheath cells, causing A to be near saturation under current C_a [Hatch, 1987; Ghannoum *et al.*, 2000].

[4] In contrast to the direct stimulation of A by elevated C_a , the reduction of moisture stress as a side effect of the widely observed decrease in stomatal conductance (g_s) under elevated C_a [Medlyn *et al.*, 2001; Ainsworth and Rogers, 2007] may play a role in augmenting A for both C3 [Medlyn *et al.*, 2001; Ainsworth and Long, 2005] and C4 [Ghannoum *et al.*, 2000; Leakey *et al.*, 2004] plants. Stomatal conductance has been shown to decrease on average

approximately 20% for a range of C3 and C4 plant species exposed to elevated CO₂ concentrations within the range 475–600 [ppm] [Medlyn *et al.*, 2001; Long *et al.*, 2004; Ainsworth and Long, 2005], which acts to balance the ratio of intercellular CO₂ concentration (C_i) to that of the external concentration [Long *et al.*, 2004]. This decrease is consistent with simple semiempirical models relating g_s linearly to the product of assimilation rate and leaf surface relative humidity, and inversely proportional to leaf surface CO₂ concentration [Ball *et al.*, 1987; Collatz *et al.*, 1991]. This ecophysiological response generally does not acclimate [Long *et al.*, 2004], remaining consistent over long-term growth under elevated C_a .

[5] Numerous leaf- and plant-level acclimations have been observed for vegetation grown in an enriched C_a environment. Amongst the most likely leaf-level changes to modify carbon assimilation is the down-regulation in Rubisco amount and/or activity (biochemical acclimation) [Stitt, 1991; Sage, 1994; Drake *et al.*, 1997] that drives a decrease in the maximum carboxylation velocity of Rubisco (V_{cmax}). The degree to which photosynthetic down-regulation may modify canopy-scale carbon assimilation remains an open question [Long *et al.*, 2004], as Ribulose 1,5-bisphosphate (RuBP) regeneration-limited (light-limited) photosynthesis can account for a large fraction of canopy carbon uptake [see Long *et al.*, 2004].

[6] At the plant-scale, structural characteristics such as plant height, stem diameter and leafing number have been found to increase for certain C3 species under elevated C_a [Ainsworth and Long, 2005]. Modifications to the foliage density (structural acclimation) has the potential to alter the radiative, micrometeorological and hydrological regimes of vegetation canopies. An increase in foliage density will likewise alter the source densities (sink is a negative source density) of CO₂, water vapor and heat. Structural, biochemical and ecophysiological acclimation under elevated C_a also have potentially significant consequences for the partitioning of energy by a vegetation canopy. Reduction in stomatal conductance acts to raise leaf temperature, resulting in greater dissipation of available energy by sensible rather than latent heat flux [e.g., Kimball *et al.*, 1994; Triggs *et al.*, 2004; Yoshimoto *et al.*, 2005; Bernacchi *et al.*, 2007]. Conservation of soil moisture due to stomatal closure and reduced transpiration can result in greater resiliency to drought under elevated C_a during periods that would otherwise result in a reduction in transpiration and carbon uptake [Wullschleger *et al.*, 2002; Hungate *et al.*, 2002; Bernacchi *et al.*, 2007].

[7] Untangling the roles of each observed acclimation in canopy-scale flux responses to elevated C_a is a challenge that will not yield easily to data alone. Due to the limited extent of FACE rings (~20 m diameter), standard flux

measurement techniques such as eddy-covariance are not applicable [Bernacchi *et al.*, 2007]. Observations of changes in photosynthetic uptake at FACE sites are typically performed on upper canopy leaves [Ainsworth and Long, 2005], leaving open the question as to how the observed responses, localized with respect to position in the canopy, will scale to produce canopy-level estimates of change. Likewise, the broad array of changes observed at FACE sites produces correlations among changes in traits, but does not necessarily indicate cause-effect relationships. It is therefore necessary to utilize the information derived from FACE sites in conjunction with models containing sufficient detail to capture the critical responses to environmental change.

[8] Here we apply this approach toward understanding the effects of elevated C_a on changes in canopy states (i.e., leaf temperature (T_l) and stomatal conductance) and fluxes (net carbon flux (A_n), latent (LE) and sensible heat (H)) within two dense plant canopies differing with respect to photosynthetic pathway and observed acclimation to growth at elevated C_a . Soybean (*Glycine max*) utilizes the C3 photosynthetic pathway, and has been shown to exhibit increases in leaf area index (LAI) [Dermody *et al.*, 2006, 2008] and a reduction in leaf carboxylation capacity (V_{cmax}) when grown in elevated CO₂ [Ainsworth *et al.*, 2002; Bernacchi *et al.*, 2005a]. Maize (*Zea mays*) utilizes the C4 pathway with no observed significant structural acclimation or reduction in photosynthetic capacity under elevated CO₂. These contrasting properties, along with the wealth of data provided by the SoyFACE experimental facility [Ort *et al.*, 2006], provide a unique opportunity to couple observations with a highly detailed mechanistic canopy model [Drewry *et al.*, 2010] to understand and extrapolate observed environmental change. Here we apply a multilayer canopy-atmosphere exchange model (MLCan) that was previously validated for both maize and soybean using multiseason eddy-covariance records of net ecosystem exchange of CO₂ and latent and sensible heat collected at an Ameriflux site in central Illinois [Drewry *et al.*, 2010].

[9] Section 2 briefly reintroduces the MLCan framework described in part 1 [Drewry *et al.*, 2010] (section 2.1), describes the FACE site (section 2.2) and discusses observed structural and biochemical acclimation of soybean and its implementation in the model (section 2.3). Results are then presented (section 3), beginning with analyses of the impact of structural acclimation on the radiative (section 3.1) and hydrological (section 3.2) regimes of the canopy and implications for energy and moisture flux to the soil. Leaf-level changes in CO₂ uptake and C_i/C_a are examined in the context of $A-C_i$ relationships for the C3 and C4 biochemistry of the two crops (section 3.3). Changes in net canopy A_n , LE and H , and T_l and g_s under elevated C_a are presented relative to the fully resolved changes through the canopy, making apparent the impact of the structure of each canopy (sections 3.4 and 3.5). Attribution of the changes in fluxes and states under elevated CO₂ for soybean is made through simulations which consider (1) all observed plant acclimations, (2) stomatal adjustment and biochemical but no structural acclimation, and (3) only stomatal adjustment. We examine the control of meteorological forcing (section 3.6) and soil moisture (section 3.7) on net canopy flux changes under elevated CO₂, and extend the analysis to

projections of mean daytime changes in flux magnitudes as the ambient C_a rises from 400 to 700 [ppm] (section 3.8), a range of ambient concentrations projected for the coming century.

2. Materials and Methods

2.1. Multilayer Model Framework

[10] To conduct the simulations presented here, we utilize the multilayer canopy model (MLCan) presented in the companion paper [Drewry *et al.*, 2010] that couples above ground ecophysiological processes with below ground coupled soil-root moisture transport [Amenu and Kumar, 2008]. In that paper a set of detailed validation experiments for a soybean/maize agro-ecosystem in central Illinois, characteristic of much of the midwestern United States, were described. Eddy covariance data from the FluxNet tower in Bondville, Illinois [Hollinger *et al.*, 2005; Bernacchi *et al.*, 2005b] was used to examine the ability of the model to capture variability in CO₂, water vapor and heat fluxes for maize (2001, 2003, 2005) and soybean (2002, 2004, 2006) canopies across a range of environmental conditions spanning three growing seasons for each crop. Discretization of the canopies into 15 layers and the soil system into 11 layers was performed as by Drewry *et al.* [2010]. Leaf area density (LAD) profiles and changes in canopy LAI for soybean and maize are as specified by Drewry *et al.* [2010]. We refer readers to that paper for details on the model formulation, parameterization and validation. Here we extend that work to an analysis of the responses of soybean and maize canopies to a C_a enriched environment, utilizing the same set of half-hourly periods as were analyzed in the previous paper.

2.2. SoyFACE Experimental Facility

[11] The SoyFACE experimental facility (<http://www.soyface.uiuc.edu>) is located within the Experimental Research Station at the University of Illinois (Urbana-Champaign) (40°02'N, 88°14'W, 228 m ASL). The primary focus of the research conducted at the site is the determination of the effects of elevated C_a and ozone on the processes regulating ecosystem behavior and their consequences for crop growth and yield [Ort *et al.*, 2006]. Free Air Carbon Enrichment [Lewin *et al.*, 1994; Miglietta *et al.*, 2001] provides a technique for experimental modification of the ambient environment under fully open-air field conditions, bypassing the problems inherent with the use of enclosures, such as restrictions to root volume and modified ambient environment [Long *et al.*, 2006; Ainsworth *et al.*, 2002; McLeod and Long, 1999]. We rely on results from multiple campaigns carried out at the SoyFACE site over several growing seasons to examine the ability of MLCan to accurately respond to leaf and canopy level changes under elevated C_a . For a detailed description of the SoyFACE experimental facility and experimental protocols used at the site we refer to Rogers *et al.* [2004] and Dermody *et al.* [2006].

2.3. Soybean Structural and Biochemical Acclimation

[12] Soybean has been observed at SoyFACE to respond to elevated C_a through both structural and biochemical acclimation. An approximate 10% increase in canopy LAI is consistently observed under elevated C_a at SoyFACE

[Dermody *et al.*, 2006, 2008]. This structural change has the potential to impact the radiative, microclimatic and hydrological environment of the canopy, and thus may play a role in canopy-level responses to elevated C_a . In order to account for this structural modification, a 10% increase in LAD was specified for each soybean canopy layer for the duration of each simulation conducted for elevated C_a .

[13] Photosynthetic down-regulation in soybean leaves has been observed as a statistically significant decrease in V_{cmax} by 4% and 6% at $C_a = 550$ [ppm] in seasonal sampling performed in 2001 and 2002 [Bernacchi *et al.*, 2005a], respectively. No effect of elevated C_a on the maximum rate of electron transport (J_{max}) was observed in either year. This reduction in V_{cmax} effectively reduces the slope of the initial portion of the $A-C_i$ curve (i.e., at lower internal CO₂ concentration) [Bernacchi *et al.*, 2005a]. A 5% decrease in V_{cmax} at 25°C was specified for soybean under elevated C_a to account for the observed down-regulation.

[14] To our knowledge, no significant structural or biochemical acclimation has been observed for maize growing in open-air field conditions under elevated C_a . We therefore prescribe no change to leaf area or biochemical parameters for the elevated C_a maize simulations. In analysis of stomatal response at elevated C_a , Leakey *et al.* [2006a] found that there is no acclimation of stomatal conductance (g_s) parameters for soybean. In the absence of a similar study for maize, stomatal conductance parameters remain unchanged from the values used for ambient C_a simulations [Drewry *et al.*, 2010].

3. Results and Discussion

[15] The results presented here compare identical model runs for current and elevated C_a , with appropriate acclimatory responses for soybean specified as described above. All responses (represented by the symbol Δ) are calculated as the difference between the value calculated at elevated C_a (550 [ppm]) and that calculated using the current C_a (370 [ppm]).

3.1. Structural Acclimation Effects on Canopy Radiation Environment

[16] The increase in canopy LAI results in greater absorption of shortwave radiation at the canopy top where the peak LAD resides (Figure 1a). The increased peak LAD at the canopy top increases shading of the leaf area below $z/h = 0.7$, where z is the vertical coordinate and h is the canopy height [m], resulting in reduced absorption lower in the canopy. The overall effect is an increase in peak canopy SW_{abs} by approximately 14 [W m⁻²] at solar noon (Figure 1b). The reduction in shortwave radiation reaching the soil surface results in a negative change in soil heat flux (G [W m⁻²]) (Figure 1c). The mean calculated reduction in G is within one standard deviation of the mean determined from the closed-canopy observational study periods at SoyFACE [Bernacchi *et al.*, 2007], with the observed and calculated mean ΔG values showing good agreement. The reduction in soil heat flux will have the effect of producing a cooler upper soil profile, with potential impacts on soil decomposition and respiration rates [e.g., Luo *et al.*, 2001; Lloyd and Taylor, 1994; Pendall *et al.*, 2004].

[17] When not considering structural acclimation for soybean (black contours in Figures 2a and 2b), the magni-

tudes of absorbed (LW_{abs}) and emitted (LW_{emit}) longwave changes are similar to those of maize (Figures 2c and 2d), with slightly higher values for maize due to greater leaf temperature (T_l [°C]) increases under elevated C_a (discussed below). The greatest change for both canopies occurs in the region where the LAD maximum and the region of maximum increase in leaf temperature are collocated. With no structural changes to the canopy the change in LW_{emit} is due solely to the leaf temperature increase by way of stomatal closure under elevated C_a . The change in LW_{abs} for maize is the result of absorption of increased LW_{emit} by the canopy. The greater increase in T_l for maize results in greater LW_{emit} , particularly in the upper canopy, with greater absorption by the foliage residing below. With the structural increase in LAI , the soybean canopy absorbs more incoming SW during daytime hours (see Figure 1), and absorbs more longwave from the sky, soil and surrounding foliage through the entire diurnal cycle, which also results in greater emission throughout the diurnal cycle (b).

3.2. Structural Acclimation Effects on Canopy Hydrology

[18] A second impact of the structural acclimation observed in soybean is the potential for the modification of canopy and soil hydrological states. The 10% increase in canopy LAI increases the canopy interception capacity for both precipitation and dew formation, resulting in greater mean accumulated water storage on leaf surfaces over the diurnal cycle (Figure 3a). The largest accumulation begins in the evening and grows until the morning hours when evaporation begins to remove the intercepted water. This change in the incremental increase in intercepted water and evaporation (Figures 3b and 3d) are correlated during the day when evaporation causes a reduction in intercepted moisture. This reduction is greatest in the upper canopy where the dense foliage has the greatest interception capacity. The contours overlain on the change in incremental water storage represent regions of increase in condensation caused by structural acclimation.

[19] A net effect of the increased foliage is a reduction in the daily total precipitation reaching the ground ($P_{g,day}$ [mm]). For small rain events, as much as 10% of the incoming rainfall is captured by the denser canopy under elevated C_a (Figure 3c). The extra interception capacity under elevated C_a captures a much smaller fraction of the large rain events.

[20] Sections 3.1 and 3.2 demonstrate the impact of structural acclimation, through the increase in canopy LAI under elevated C_a . Shortwave attenuation becomes greater in the upper canopy, resulting in increased shading and reduced soil heat flux. Greater moisture capture likewise results in a reduction of throughfall to the soil system, potentially significant for small precipitation events. The role of structural acclimation, along with ecophysiological and biochemical acclimation, will be examined for canopy fluxes and states in the following sections.

3.3. Leaf-Level CO₂ Flux and Internal CO₂ Concentration

[21] Leaf-level responses to environmental perturbations provide an indication of how certain regions of a plant canopy may respond to specific forcing conditions. In the context of SoyFACE, several campaigns examining the

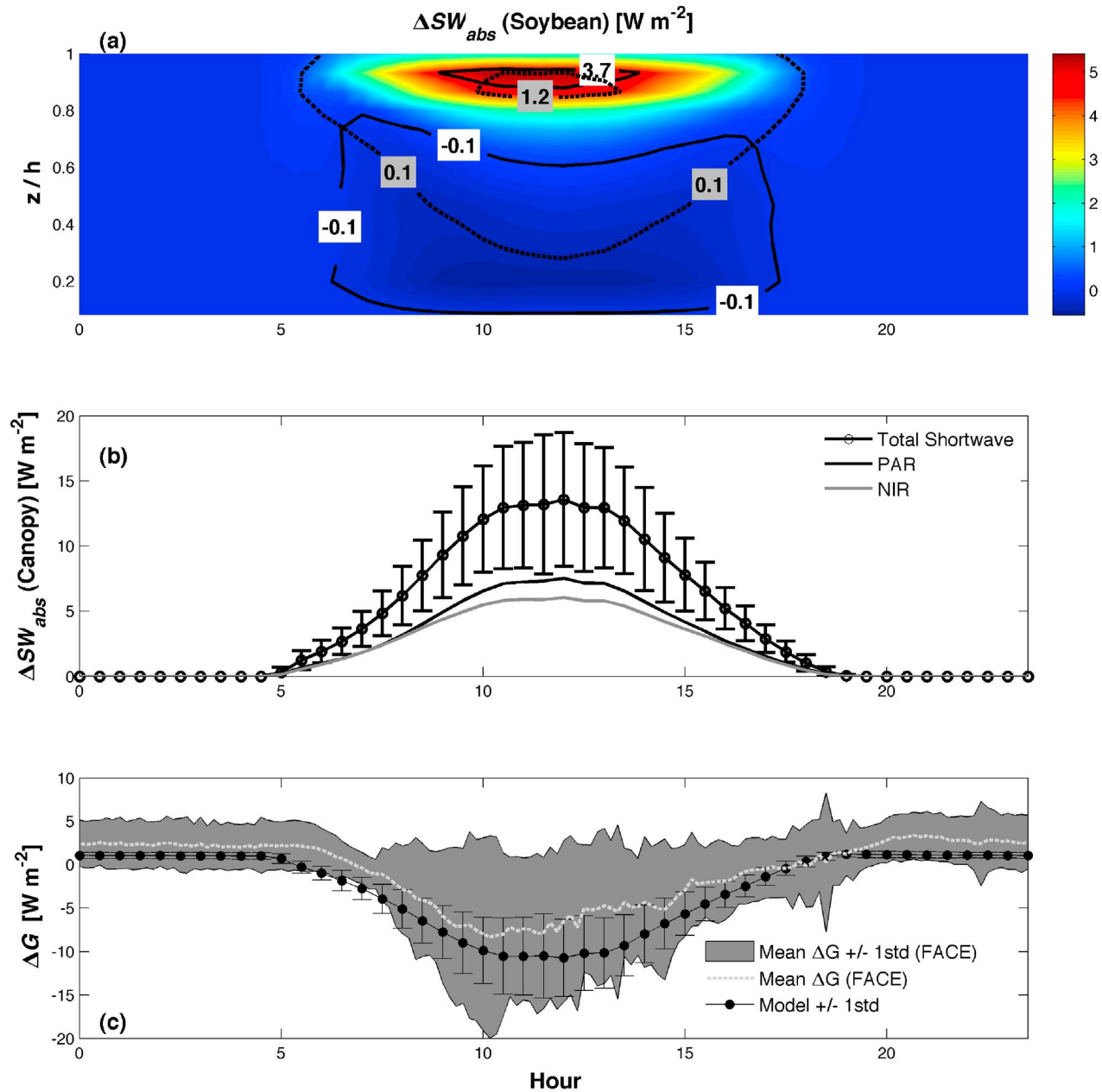


Figure 1. The effect of soybean structural acclimation on the canopy shortwave regime and soil heat flux. (a) The mean diurnal change (difference between elevated and current C_a simulations) in absorbed shortwave resolved through the canopy space. Contours depict changes for PAR (solid black) and NIR (dashed black). (b) The integrated, or total canopy change in absorbed shortwave. (c) The simulated change in soil heat flux \pm one standard deviation (black line/dots). The mean observed change in 2004 and 2006 [Bernacchi *et al.*, 2007] is presented as the dashed gray line, with \pm one standard deviation of the observed change indicated by the dark-gray shaded region.

photosynthetic capacity and stomatal conductance of canopy-top leaves grown under current (370 [ppm]) and elevated (550 [ppm]) CO₂ concentrations have been conducted. As field examinations of changes in leaf-level fluxes and states under modified environmental conditions are often conducted for the youngest fully expanded leaf at the canopy top [i.e., Morgan *et al.*, 2004; Bernacchi *et al.*, 2005a; Leakey *et al.*, 2006b], we use the topmost model layer for comparison to observed changes. The peak difference in A_n

for soybean (Figure 4a) occurs between 1200 and 1300 with a mean magnitude of 4 $[\mu mol (m^{-2} \text{ leaf area}) s^{-1}]$. The red band corresponds to a 20–30% increase in A_n relative to A_n at current C_a , from the hours 0800 to 1600. This brackets the mean observed change in canopy-top photosynthesis as determined by diurnal gas exchange measurements for seven days in 2001 (mean 24.6% daytime increase across all study days) [Rogers *et al.*, 2004], and in another set of 15 diurnal measurements carried out from 2002 to 2004

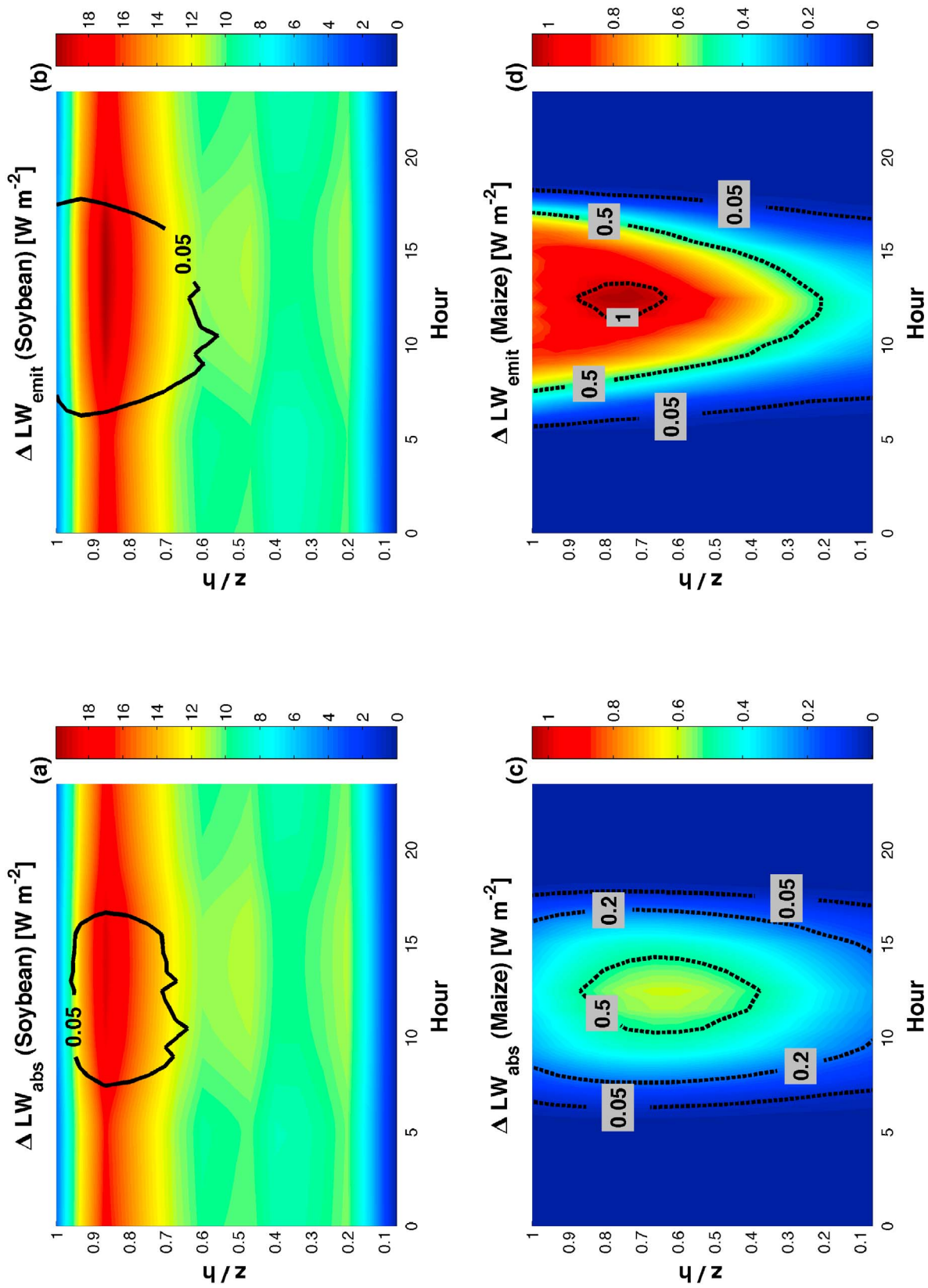


Figure 2

(mean 24% daytime increase across all study days) [Bernacchi *et al.*, 2006].

[22] The soybean response contrasts sharply with the response of canopy-top maize leaves (Figure 4b). The saturation of photosynthesis of C4 crops at current CO₂ concentrations [Jenkins *et al.*, 1989; Furbank *et al.*, 1989] makes the most likely impacts of elevated C_a on C4 crops those due to the reduction of g_s , which acts to conserve soil moisture for use during dry periods. Stomatal closure also increases leaf temperature, potentially pushing T_l closer to the photosynthetic optimum value, thereby increasing photosynthetic uptake [Ghannoum *et al.*, 2000; Ghannoum, 2009]. The opposite effect is also possible, in which T_l is increased beyond its optimum value into the region in which photosynthesis decreases with increasing T_l [Sage and Kubien, 2007]. The combined impacts of these two mechanisms during the maize simulation periods resulted in a mean mid-day stimulation in A_n of approximately 0.3 to 0.5 [$\mu\text{mol m}^{-2}$ leaf area s^{-1}], or 1 to 2.5%, under elevated C_a . No statistically significant stimulation of photosynthesis in maize at SoyFACE was found for a set of diurnal gas exchange measurements collected in 2004 [Leakey *et al.*, 2006b], despite increases up to 1.2 [$\mu\text{mol m}^{-2}$ leaf area s^{-1}] on certain sampling days. In 2002, a similar set of diurnal gas exchange observations showed average increases in photosynthesis of 10% which were attributed to improved crop water status associated with reduced transpiration under elevated C_a [Leakey *et al.*, 2004].

[23] The increase in ambient C_a does not significantly modify the diurnally averaged ratio of C_i to C_a for either crop. There is a slightly larger decrease in C_i/C_a for maize, with a midday maximum difference of approximately 0.05, consistent with a lack of significant observed change in C_i/C_a for the maize crop at SoyFACE [Leakey *et al.*, 2004, 2006b]. This indicates that the principles applied in MLCan to couple stomatal conductance, photosynthesis and leaf energy balance are capable of capturing the widely observed conservation of C_i/C_a for C3 and C4 crops [Long *et al.*, 2004; Ainsworth and Long, 2005].

[24] Synthetic A - C_i curves are constructed from the model biochemical formulation [Farquhar *et al.*, 1980; Farquhar and Sharkey, 1982] for soybean (Figure 4e) and [Collatz *et al.*, 1992] for maize (Figure 4f), using the mean Q_{abs} and T_l of canopy-top leaves across the three simulated seasons for each canopy at noon. The average increase of 4 [$\mu\text{mol m}^{-2}$ leaf area s^{-1}] in uptake at noon (Figure 4a) for soybean is indicated by the difference between the two ordinate intercepts. Despite a wider range of C_i for the elevated C_a soybean leaves ($C_i = 385$ to 470 [ppm]) relative to soybean at current C_a ($C_i = 255$ to 315 [ppm]), the range of A_n for elevated C_a is narrower (22.5 to 24.0 for elevated C_a versus 18.5 to 21.0 for current C_a). This is due to the nonlinear response of A_n to C_i for C3 plants, which causes

greater sensitivity of A to variations in C_i at lower C_i [Farquhar and Sharkey, 1982].

[25] In contrast to the C3 biochemistry of soybean, the CO₂ saturation mechanism of C4 bundle sheath cells is seen here to cause insensitivity of A to changes in C_i for the average conditions experienced by the simulated maize leaves. Only under extreme stomatal closure, in which C_i is driven below approximately 100 [ppm], would significant changes in A occur. Although difficult to see on the plot, a small 0.3 [$\mu\text{mol m}^{-2}$ leaf area s^{-1}] increase in A occurs on average at noon for maize due to the increase in leaf temperature brought about by stomatal closure under elevated CO₂.

[26] An important factor in the response of the C3 and C4 leaves to elevated CO₂ is the strength of the feedback between A and g_s . For the C4 leaves (Figure 4f), the insensitivity of A to C_i essentially decouples photosynthetic uptake from stomatal functioning except for extreme stomatal closure. For the C3 leaves (Figure 4e), increases in ambient C_a result in greater A , acting to partially offset the reduction in conductance that occurs under elevated C_a (see equation (11) in the auxiliary material of Drewry *et al.* [2010], and Ball and Berry [1982]). This results in a greater reduction in g_s for maize under elevated CO₂, as represented by the slopes of the dotted lines from the abscissa to the A - C_i curves. For the limited set of conditions examined here, there is a mean reduction in g_s under elevated C_a , relative to current C_a , of 18% for soybean, and 28% for maize.

3.4. Vertically Resolved and Canopy Integrated Diurnal Changes in Fluxes

[27] Section 3.3 examined the change in canopy-top leaf-level carbon dioxide flux when ambient C_a was increased from 370 to 550 [ppm]. Estimation of changes in canopy functioning and response to environmental change requires knowledge of how responses vary vertically through the canopy space. In order to understand how elevated C_a impacts the entire vegetation canopy, we examine here the mean diurnal changes to canopy net carbon dioxide, latent energy and sensible heat fluxes for both crops.

3.4.1. Soybean

[28] The changes in soybean canopy fluxes are presented in Figure 5. Figures 5a–5c show the vertically integrated mean diurnal changes in A_n , LE and H , where the influences of structural and biochemical acclimation are demonstrated through simulation results in which no structural change was prescribed (gray lines), and neither structural nor biochemical changes prescribed (purple lines) for the elevated C_a runs. Included are simulation results for an unobserved case in which both V_{cmax} and J_{max} are reduced by 5% (green contour lines), corresponding to a scenario in which a constant ratio of V_{cmax} to J_{max} is maintained [Wullschlegel, 1993] under biochemical downregulation. The combined downregulation of both V_{cmax} and J_{max} has not been

Figure 2. Mean diurnal changes in the longwave regime of the (a and b) soybean and (c and d) maize canopies. (left) The change in absorbed longwave radiation and (right) the change in emitted longwave radiation through the canopy. The contours on the soybean LW_{abs} (Figure 2a) and LW_{emit} (Figure 2b) panels represent simulations in which the structural acclimation for soybean was not considered, to better compare with the maize panels. Maize does not experience structural acclimation, and so changes in the longwave regime are the result of changes in T_l . One of the three contour lines on the maize panels represents the same values as the soybean contour values for comparison.

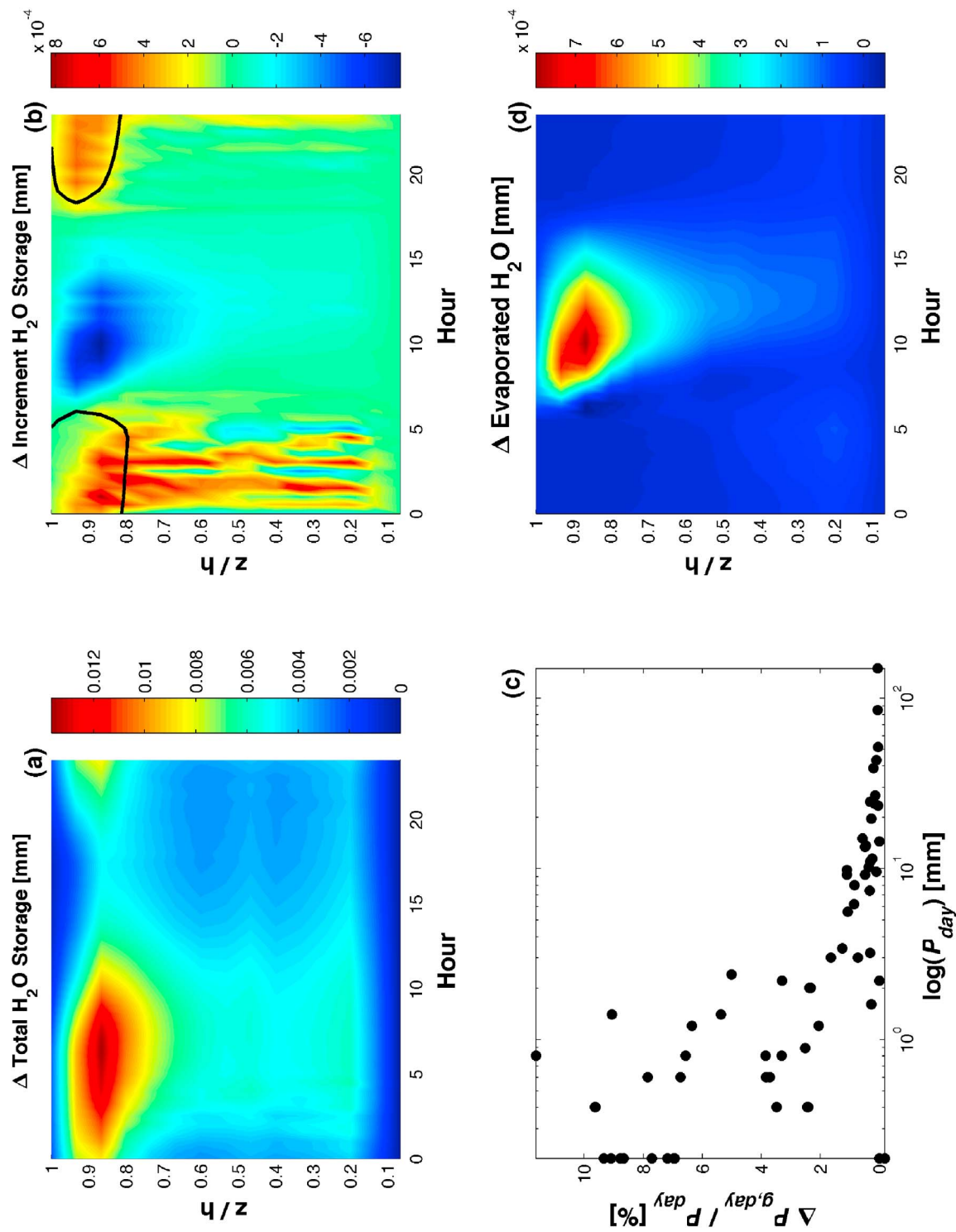


Figure 3. Mean diurnal changes in canopy hydrologic variables under elevated CO₂. (a) The change in the total water intercepted (precipitation and dew) by the canopy. (b) The change in instantaneous interception increments made to the canopy foliage. (c) The change in the percentage of total daily precipitation reaching the ground is plotted on a semilog scale. (d) The mean diurnal course of evaporation through the canopy.

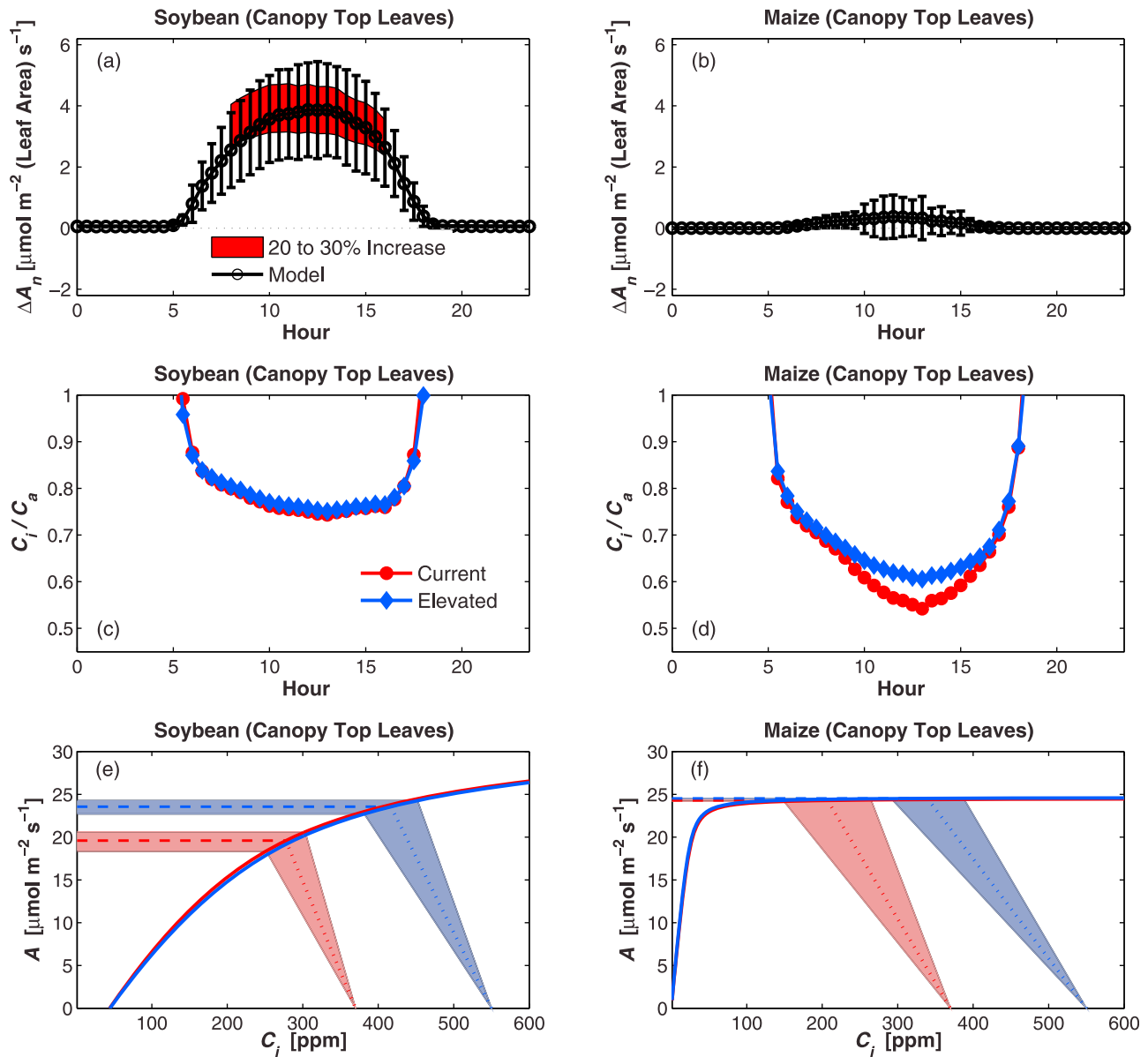


Figure 4. Leaf-level responses of photosynthesis to elevated CO₂ concentration. Figures 4a and 4b show the diurnal mean response (\pm one standard deviation) of photosynthesis per unit leaf area at the top of the (a) soybean and (b) maize canopies. The shaded red region for soybean changes represents a 20–30% increase in A under elevated CO₂, which spans the 24.6% and 24% increases in daytime photosynthesis for canopy-top soybean leaves at SoyFACE for two studies that examined diurnal gas exchange observations collectively over the 2001–2004 growing seasons [Rogers *et al.*, 2004; Bernacchi *et al.*, 2006]. Figures 4c and 4d present the mean diurnal ratios of internal to ambient external CO₂ concentrations for (c) soybean and (d) maize under elevated (blue diamonds/line) and current (red circles/line) CO₂ concentrations. Figures 4e and 4f present example synthetic A - C_i curves derived from the biochemical models applied in the multilayer canopy model [Drewry *et al.*, 2010] for (e) soybean and (f) maize for the mean noon conditions (Q_{abs} and T_l) experienced over the set of simulated seasons, under elevated (blue curves) and current (red curves) CO₂ concentrations. Dotted lines connect the ambient CO₂ concentration to the mean C_i on the curves. Horizontal dashed lines indicate the average A at the average C_i value, with shading for ± 1 standard deviation around the mean C_i value and the resulting range of calculated A values.

observed, but is included here to contrast with the observed downregulation of V_{cmax} .

[29] The combined case of structural, downregulation and ecophysiological acclimation effects (black dots/line) shows a peak increase in A_n of 7.4 [$\mu\text{mol m}^{-2} \text{s}^{-1}$], or 23.6%

(Figure 5a). When structural change is not considered, the increase in A_n is 7.2 [$\mu\text{mol m}^{-2} \text{s}^{-1}$], or 23.1%. The 10% increase in LAI has no effect except to provide a negligible increase in canopy A_n at the peak of the day, when low zenith angles allow the greatest penetration of photosyn-

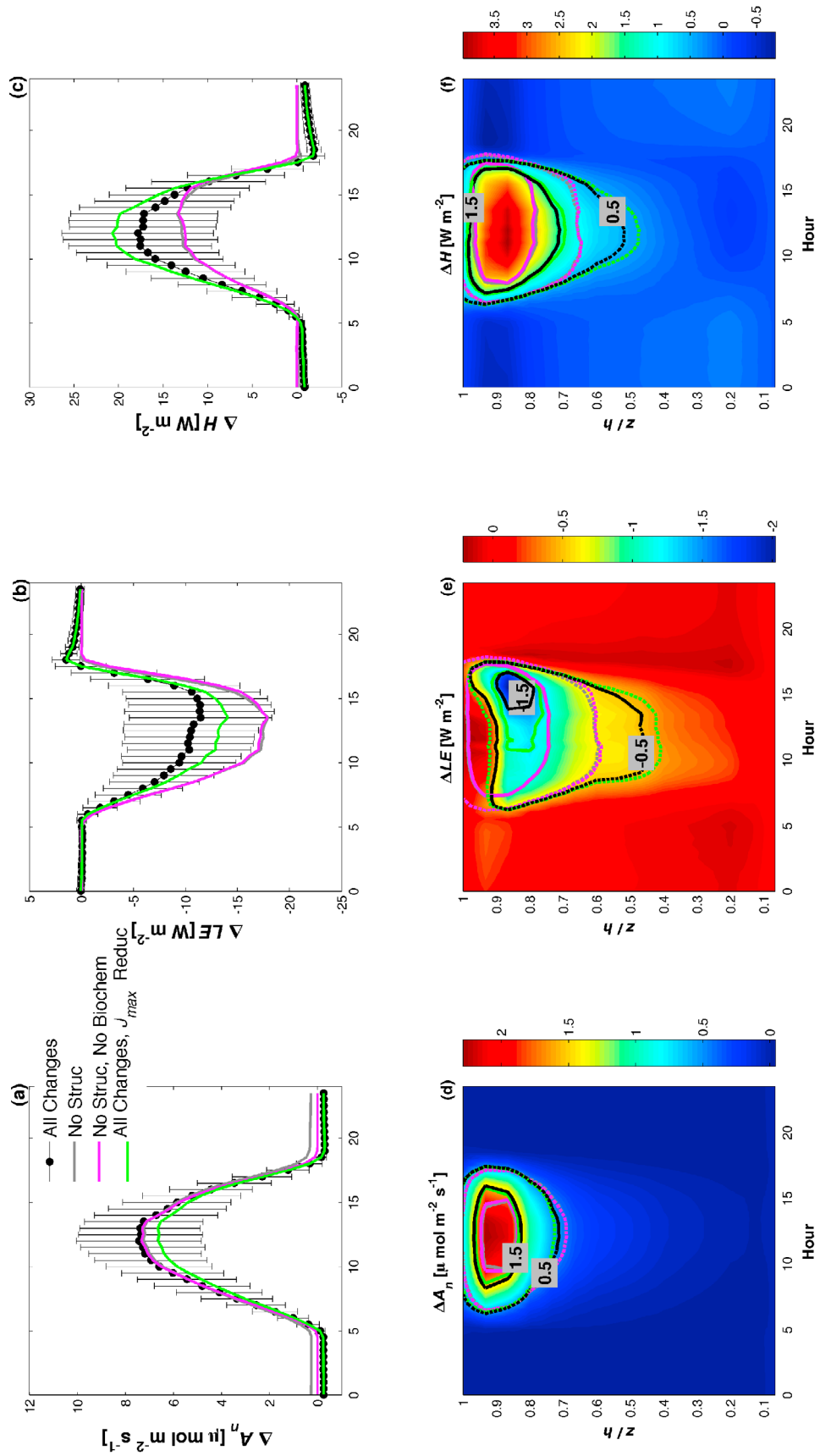


Figure 5

thetically active radiation through the denser upper foliage. Removing both structural and biochemical acclimation from consideration (i.e., only change attributable to ecophysiological reduction in g_s), A_n is nearly identical to the case in which the structural acclimation alone was removed, implying no canopy-scale effects of the down-regulation of Rubisco carboxylation capacity, providing canopy-scale agreement to the analogous leaf-level observation of no change in photosynthesis as a consequence of down-regulation [Bernacchi *et al.*, 2005a]. Biochemical and structural acclimation effects have a minor impact on the net canopy CO₂ uptake of the soybean canopy. A similar change in J_{\max} is shown to result in a reduction in canopy net carbon dioxide uptake, with a peak value of 6.6 [$\mu\text{mol m}^{-2} \text{s}^{-1}$]. This is due to a reduction of the photosynthetic capacity of light-saturated upper-canopy foliage. These results indicate that down-regulation does not impact canopy-scale photosynthesis and therefore may be due to a more efficient reallocation of photosynthetic resources.

[30] Figure 5d displays the resolved changes in A_n through the canopy. Contours for $\Delta A_n = 0.5$ (dashed lines) and 1.5 (solid lines) [$\mu\text{mol m}^{-2} \text{s}^{-1}$] are presented for the same set of simulations in the same colors as depicted in Figures 5a–5c. In the upper part of the canopy ($z/h \simeq 0.9$), the $A_n = 1.5$ contours show a constriction of the region of high photosynthesis when the structural acclimation is removed, due to the reduction in photosynthesizing foliage in the upper canopy (see Figure 1). The reduction in SW_{abs} in the upper canopy when structural acclimation is not considered causes an increase in shortwave penetration to the lower canopy where photosynthesis is light-limited, resulting in increased photosynthesis below the LAD maximum ($A_n = 0.5$ contour). Thus, the net effect of the structural acclimation is negligible, with the primary effect being a vertical shift in the carbon dioxide sink distribution. Biochemical down-regulation has little effect through the canopy, demonstrated by the overlapping contours representing no structural acclimation, and no structural and no biochemical down-regulation. The lower canopy is light-limited precluding any effect due to the modification of V_{cmax} .

[31] LE decreases at noon by approximately 11.5 [W m^{-2}] when all soybean acclimations are considered, in contrast to an 18 [W m^{-2}] reduction when the foliage is not augmented (Figure 5b). The increase in LAI provides more leaf area for transpiration, increasing the mean midday water flux by approximately 7 [W m^{-2}] as seen by the additional decrease in LE if structural acclimation is not considered. A reduction in J_{\max} causes a reduction in A_n which reduces stomatal conductance [see Drewry *et al.*, 2010, Figure 2] and thereby reduces LE by 3 [W m^{-2}] relative to ecophysiological acclimation alone. Figure 5e shows the regions of greatest reduction in LE (-1.5 [W m^{-2}] contour) is expanded upward to the canopy top when the structural acclimation is not

considered. The added leaf area at the canopy top produces the greatest contribution to increases in LE under elevated C_a , relative to the case where no structural acclimation occurs. Structural acclimation plays a significant role in offsetting the reduction in LE caused by ecophysiological and biochemical acclimation, reducing the mean response by approximately 40% at midday.

[32] The noon increase in H is 17.5 [W m^{-2}] when all acclimations are considered (Figure 5c). Here the ecophysiological attributable change at noon (12.5 [W m^{-2}]) is increased by 44% due to the structural augmentation of the canopy. Figure 5f shows the region of greatest increase is highly correlated with the region of greatest increase in SW_{abs} (see Figure 1), as was the region of greatest increase in A_n . This region in the upper canopy shrinks when either the increase in LAI is neglected in this highly active part of the canopy. Similar effects are seen lower in the canopy through the $\Delta H = 0.5$ [W m^{-2}] contour.

3.4.2. Maize

[33] Elevated C_a causes a slight mean increase in A_n during the day (Figure 6a), a peak decrease in LE of 50 [W m^{-2}] (Figure 6b), and a peak increase in H of 45 [W m^{-2}] (Figure 6c). The mean daytime increases in A_n are attributed to reductions in g_s that drive T_l slightly closer to the photosynthetic optimum value. The mean changes in canopy energy flux are significantly larger than those for soybean (see Figure 5). This is due in part, for the case of LE , to the lack of structural or biochemical acclimation in maize that was seen to offset the reduction in LE for soybean under elevated C_a by increasing the transpiring leaf area. For both canopies the ecophysiological reduction in g_s under elevated C_a increases T_l through the canopies and thereby shifts energy dissipation from LE to H . A primary factor in the different responses of soybean and maize energy fluxes to elevated C_a is the direct stimulation of A_n by elevated CO₂ concentrations for soybean. This greater increase in A_n raises stomatal conductance, diminishing the reduction in g_s from ecophysiological adjustment. For maize, the negligible increase in A_n has no impact on the ecophysiological adjustment experienced by stomates. Figures 6d–6f show that the region of greatest change through the maize canopy is at the canopy top, with the changes decreasing smoothly downward through the canopy for all three fluxes, due to the relatively uniform and smooth distribution of maize leaf area.

3.5. Vertically Resolved and Mean Diurnal Changes in T_l and g_s

[34] The changes in canopy fluxes due to elevated C_a are in large part controlled by the ecophysiological acclimation of stomates. In this section we examine the changes to leaf temperature and stomatal conductance relative to observa-

Figure 5. Modification in canopy-integrated and canopy-resolved canopy-atmosphere fluxes for soybean. The mean canopy diurnal fluxes (Figures 5a–5c) of (a) carbon dioxide, (b) latent energy, and (c) sensible heat are presented as black dots, with black bars indicating \pm one standard deviation. Gray and purple lines present the same mean fluxes for simulations in which the structural acclimation (gray), or both structural and biochemical acclimation (purple), were not considered. Figures 5d–5f show the resolved flux magnitudes through the canopy space. The fluxes of (d) carbon dioxide, (e) latent heat, and (f) sensible heat are shown. Contours correspond to simulation results conducted considering all acclimations (black), no structural acclimation (gray), no structural and no biochemical acclimation (purple), and all acclimations with J_{\max} also reduced (i.e., assuming a constant ratio of $V_{\text{cmax},25}$ to $J_{\max,25}$ between current and elevated C_a cases; green).

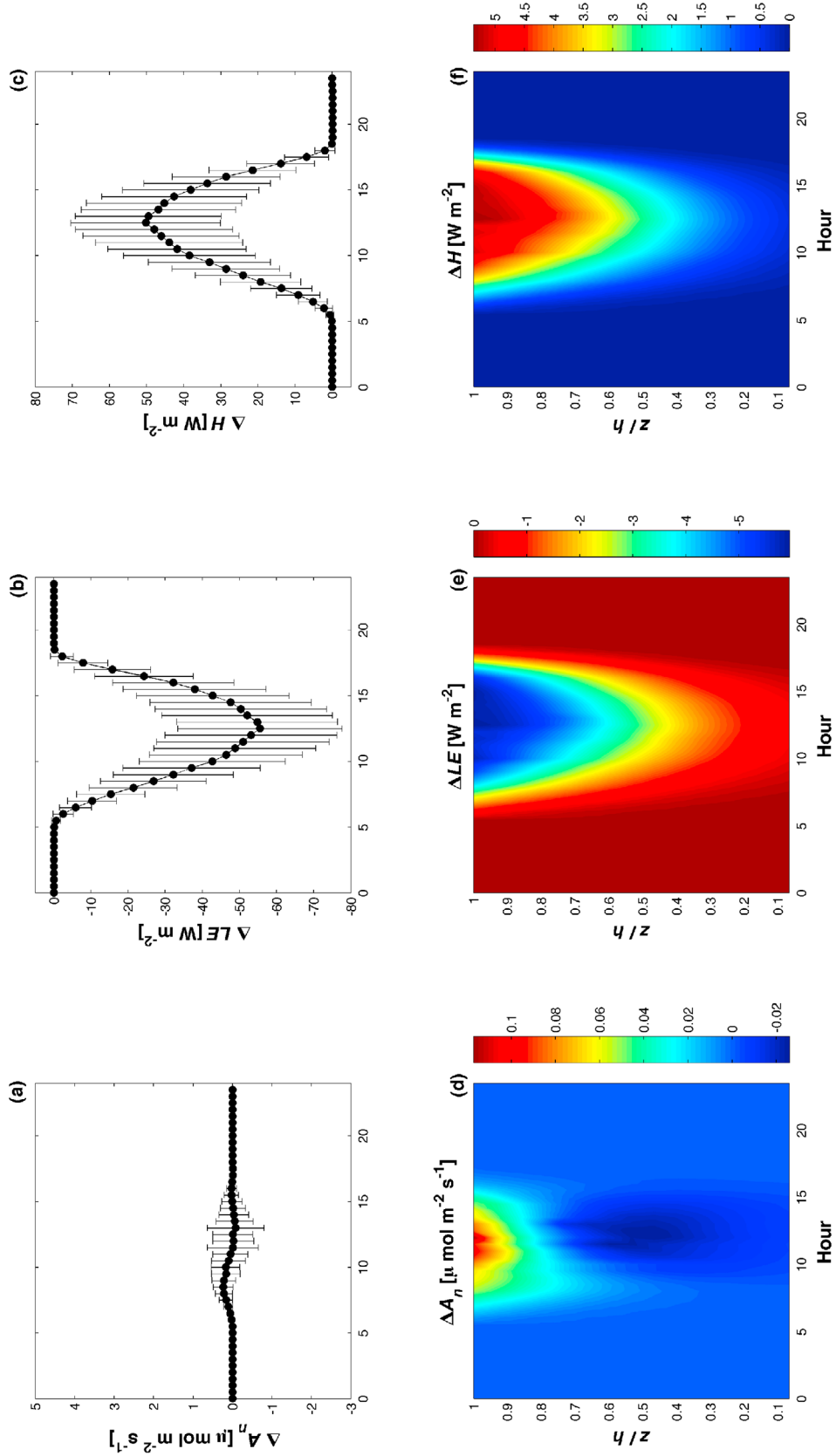


Figure 6. Modification in canopy-integrated and canopy-resolved canopy-atmosphere fluxes for maize. The plot structure is identical to that of Figure 5, which examined changes in canopy fluxes for soybean. No structural or biochemical acclimation has been observed for maize at SoyFACE, and therefore simulations were conducted for these cases and no contours plotted.

tions at the canopy top and vertically resolved through the canopy.

3.5.1. Soybean

[35] The mean diurnal changes in leaf temperature and stomatal conductance for the soybean canopy under elevated C_a are presented in Figure 7. Figure 7a presents the canopy-top increase in leaf temperature (black line/dots) ± 1 standard deviation, along with the mean (light gray line) and ± 1 standard deviation spread about the mean (dark gray shaded region) diurnal canopy ΔT_l as observed with infrared temperature (IRT) sensors at the SoyFACE site through the 2003–2006 growing seasons [Bernacchi *et al.*, 2007]. The calculated canopy-top value is well within one standard deviation of the observations for all time periods, despite a discrepancy of approximately 0.2°C for midday upper canopy leaf temperature. The spread of the observed values indicates that there may have been significant spatial variability between the four sampled pairs of FACE rings in ΔT_l during the observation periods.

[36] The LAD -weighted canopy mean leaf temperature change (red line) is approximately 0.15°C lower at midday than the calculated values for canopy-top foliage. Figure 7c shows strong vertical variation in ΔT_l during midday when photosynthesis is most active and stomatal conductance is highest. Leaf temperature at the bottom of the canopy is reduced due to the reduction in radiation reaching the lower canopy levels from the effects of structural acclimation.

[37] The canopy-top diurnal mean change in g_s along with the canopy average is shown in Figure 7b. Rogers *et al.* [2004] found a 21.9% decrease in canopy-top, midday g_s over the course of several study days in 2004. In a similar set of observations, Bernacchi *et al.* [2006] analyzed 15 sets of diurnal gas exchange measurements and found a 16% decrease in canopy-top g_s , with 53% of the study days showing a statistically significant decrease. The calculated midday canopy-top changes are within this range of observed change as depicted by the blue region spanning a 15 to 25% reduction in g_s relative to the current C_a simulation. The LAD -weighted canopy-average change in g_s is lower than the canopy-top values by more than a factor of two as a result of the large vertical variability. The resolved change in g_s over the diurnal period (Figure 7d) shows strong vertical variation in g_s during daytime photosynthetic activity, with canopy-top changes the greatest.

[38] Figures 7c and 7d have three sets of contours, at two T_l and g_s values, to demonstrate the impact of structural and biochemical acclimation, as was done in section 3.4.2 for the analyzed scalar fluxes. The structural acclimation pro-

duces the largest effect on lower canopy T_l due to the modified radiation regime. Removing the structural acclimation allows greater SW penetration deeper into the canopy. This has two primary effects. Enhanced absorption of both photosynthetically active and near infrared radiation acts to raise the temperature of the foliage deeper in the canopy. The photosynthetically active portion excites light-limited photosynthesis deep in the canopy, increasing g_s by way of the linear dependence of g_s on photosynthesis [Ball *et al.*, 1987], and thereby decreasing Δg_s .

3.5.2. Maize

[39] The mean simulated canopy-top ΔT_l and IRT observations for maize compare very well through the course of the day (Figure 8a). The LAD -weighted mean change in T_l is approximately 0.25°C lower than the computed canopy-top change. There is strong variation in the temperature change through the canopy, with the range of temperature changes spanning 0.5 degrees from the bottom to top of the canopy at midday (Figure 8c). As for the soybean, this is primarily due to the greater photosynthetic activity in the upper canopy that drives stomatal conductance, which is significantly reduced by ecophysiological acclimation. The maximum canopy-top temperature increase for maize is about 0.7°C, compared to 0.2°C for soybean. This can be explained in part by the direct stimulation of A_n for the C3 crop. Increasing A_n increases g_s and therefore lowers the impact of the ecophysiological reduction of g_s as C_a is increased.

[40] The mean noon decrease in g_s at the canopy top for maize is approximately $-0.1 \text{ [mol m}^{-2} \text{ s}^{-1}]$ relative to -0.07 for soybean (Figure 8b). This difference is partially the result of greater direct stimulation of A_n for the C3 soybean crop which decreases Δg_s . Leakey *et al.* [2006b] found an average midday reduction of 34% for g_s of canopy-top maize leaves at SoyFACE in 2004, a year in which the crop experienced no water stress. The blue shaded region under the canopy-top change plot in Figure 8b represents a 28 to 38% decrease in stomatal conductance for the middle of the day, within which the model estimated changes lie.

3.6. Meteorological Control of Canopy-Atmosphere Exchange Responses

[41] The effect of leaf acclimatory responses to elevated C_a have been shown to be correlated with ambient meteorological forcing conditions [Bernacchi *et al.*, 2006]. To examine the effect of the primary meteorological drivers on canopy-atmosphere exchange the average daytime ($R_g > 10 \text{ [W m}^{-2}]$) change in canopy net carbon dioxide, latent

Figure 7. Modification of diurnal mean canopy leaf temperature and stomatal conductance for the soybean canopy under elevated C_a . Figures 7a and 7b present canopy-top changes in (a) leaf temperature and (b) stomatal conductance. Calculated means \pm one standard deviation are given as black dots/lines, and leaf area density-weighted canopy mean changes are presented as red lines. The mean observed change in T_l using IRT sensors placed above the soybean canopy at SoyFACE in 2004 and 2006 [Bernacchi *et al.*, 2007] are presented as the light gray line, with the mean \pm one standard deviation region specified by dark gray shading. The range representing a 15–25% reduction in mean canopy-top stomatal conductance, relative to the calculated ambient values, during midday (0800–1600) is presented as the blue shaded region. This range of midday Δg_s corresponds to the magnitudes of observed changes in soybean canopy-top g_s at SoyFACE [Rogers *et al.*, 2004; Bernacchi *et al.*, 2006]. Figures 7c and 7d present the changes in (c) T_l and (d) g_s through the canopy. As for the case of soybean fluxes (Figure 5), contours correspond to simulation results conducted considering all acclimations (black), no structural acclimation (gray), no structural and no biochemical acclimation (purple), and all acclimations with J_{\max} reduced also (i.e., assuming a constant ratio of $V_{c\max,25}$ to $J_{\max,25}$ between current and elevated C_a cases; green).

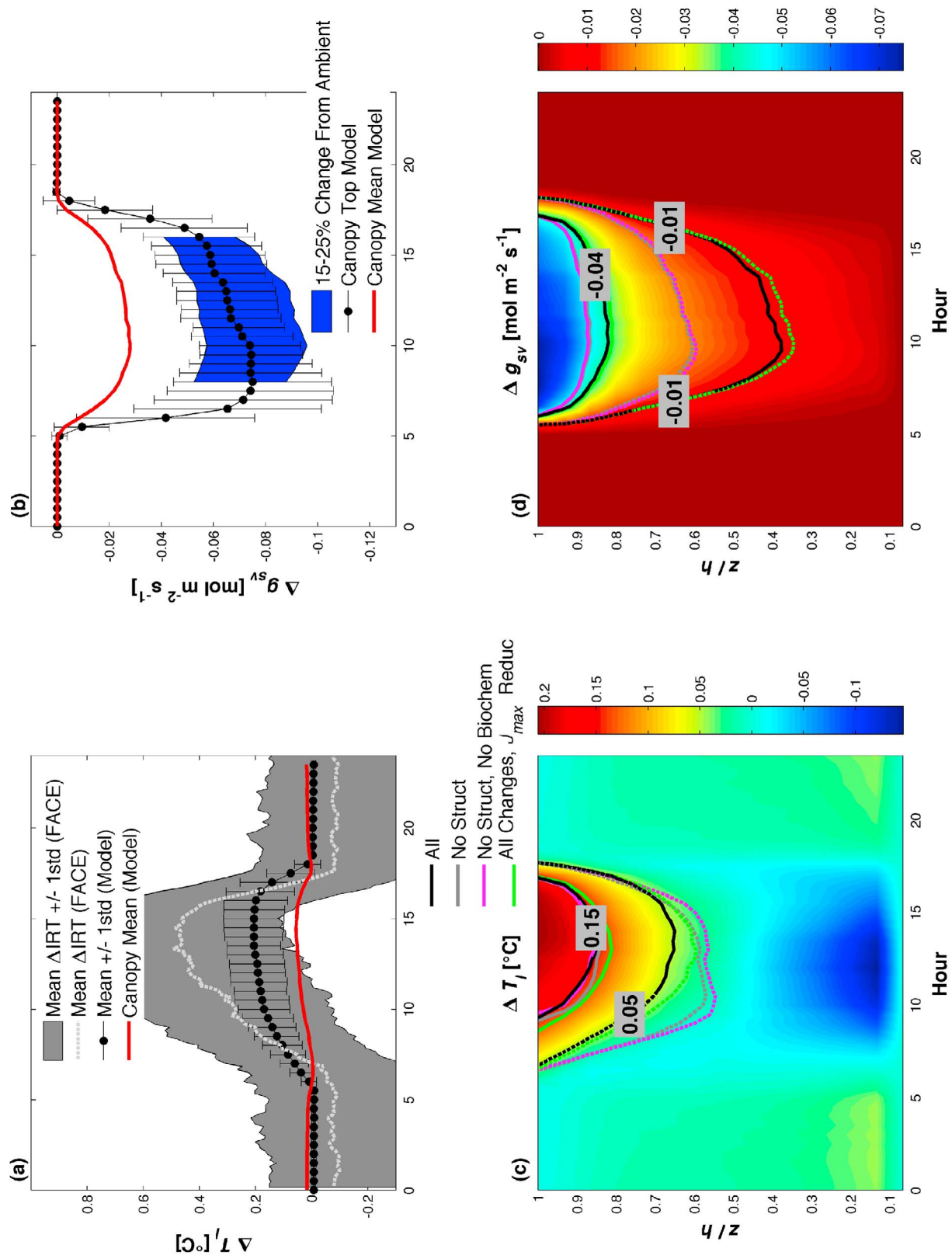


Figure 7

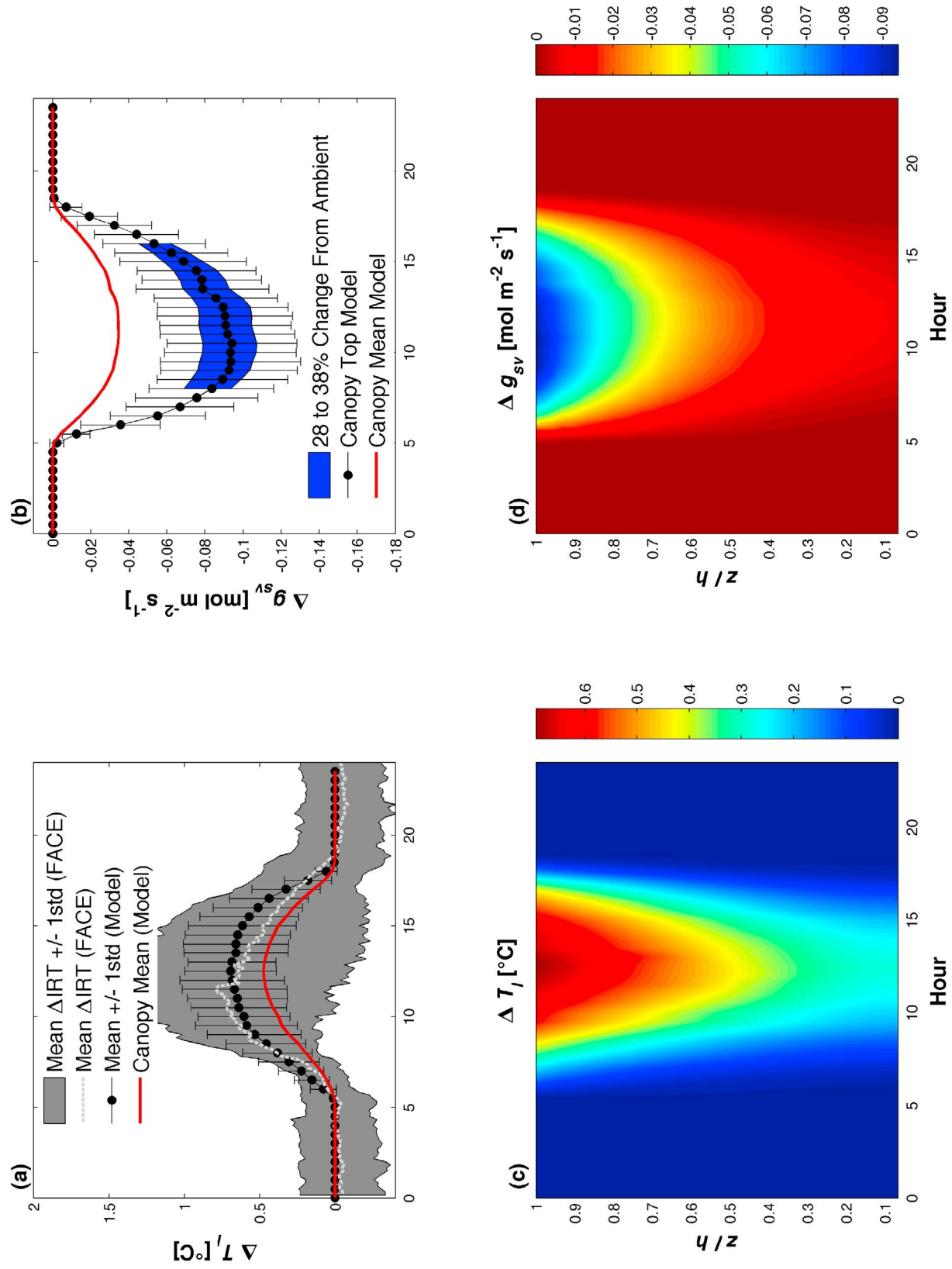


Figure 8

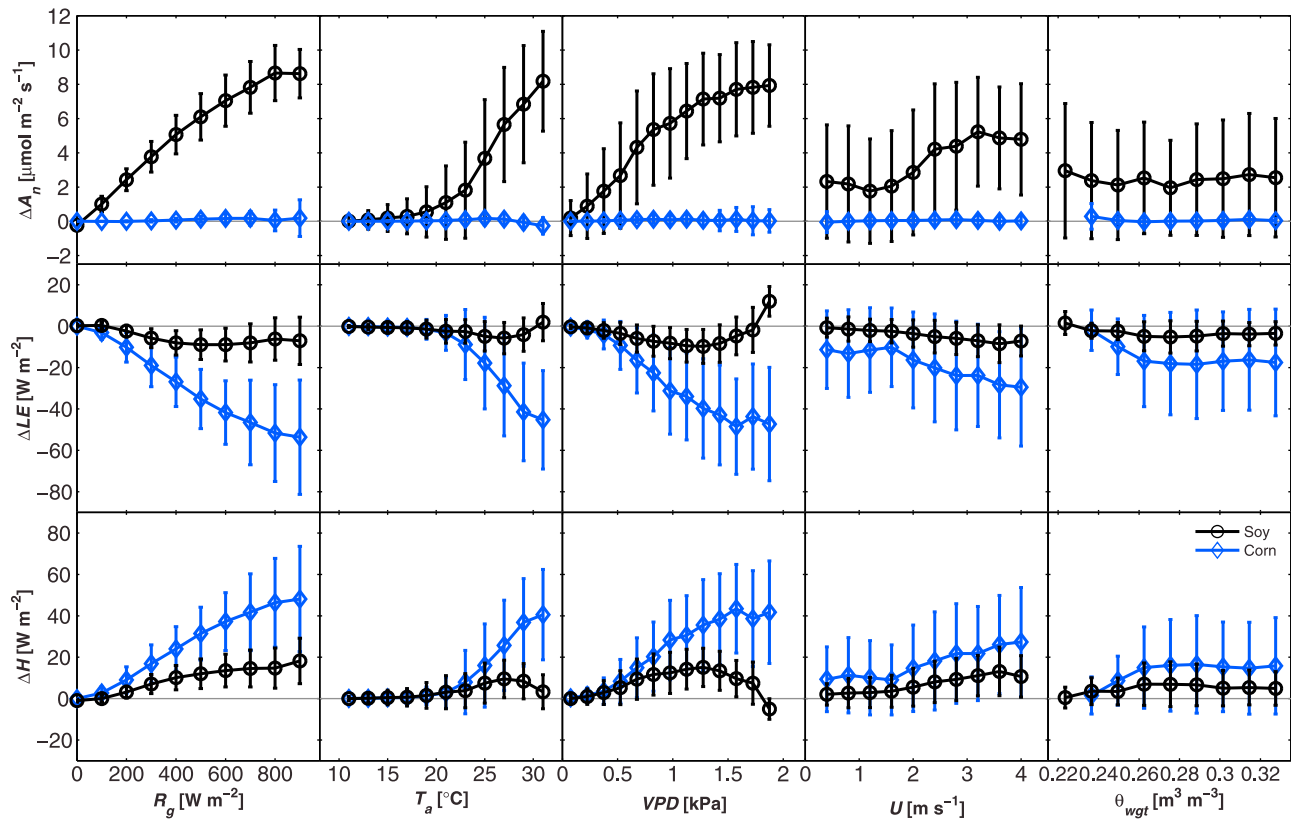


Figure 9. Variation in the daytime changes in soybean (circles, black lines) and maize (diamonds, blue lines) with observed meteorological forcing and soil moisture status. Average changes in net (top) carbon dioxide exchange, (middle) latent heat fluxes, and (bottom) sensible heat fluxes for the two crop canopies under elevated C_a , relative to current C_a (left to right). The changes with respect to incoming shortwave radiation, air temperature, vapor pressure deficit, wind speed, and root profile-weighted soil moisture, are presented. Flux changes are calculated for those periods for which $R_g > 10$ [W m^{-2}]. Vertical bars represent one standard deviation above and below the mean values (symbols).

energy and sensible heat fluxes were calculated across ranges of R_g , T_a , VPD and U . In Figure 9, the mean \pm one standard deviation flux change across the range of meteorological conditions experienced for each of the three study years for each crop are plotted. The changes with respect to root profile weighted soil moisture (θ_{wgt}) are also presented.

[42] Maize A_n has a negligible response across all meteorological conditions. There is a mean positive change in CO_2 uptake for high R_g , likely due to covariation of R_g with T_a . At the highest air temperatures, the slight increase in maize A_n is lost as the leaf temperature increases past the photosynthetic optimum. There is a slight increase in ΔA_n for low soil moisture as the moisture conserved by reduced stomatal aperture enables CO_2 uptake when plants in current ambient conditions experience moisture stress.

[43] The change in carbon dioxide uptake for soybean increases almost linearly with increasing R_g through the range of values experienced in the three study years. This

effect saturates at the highest R_g values as most radiation is captured by the upper canopy LAD maximum, where the foliage is primarily light saturated (see Figure 5). There is a clear effect of covariation with R_g in the responses to T_a , VPD and U . A slight increase under low soil moisture conditions is also apparent, as was the case for maize, as water conservation due to the ecophysiological adjustment allows for a relative increase in carbon uptake when the current C_a plants are water stressed.

[44] The change in maize LE decreases near linearly with increasing R_g , with a similar covariation effect for T_a , VPD and U as was the case for soybean A_n . At high VPD the increasing trend in ΔLE is curtailed, as these high VPD values are typically correlated with reduced soil moisture. Under these conditions, ambient LE is reduced, thereby reducing the negative (elevated – current) change as transpiration under elevated C_a is unaffected. This effect is stronger for the soybean plants, as they experience greater

Figure 8. Modification of diurnal mean canopy leaf temperature and stomatal conductance for the maize canopy under elevated C_a . The plot structure is identical to that of Figure 7, which examined changes in T_l and g_s for soybean. No structural or biochemical acclimation has been observed for maize at SoyFACE, so no simulations were conducted for these cases and no contours plotted. The shaded blue region in the canopy-top g_s panel (Figure 8b) indicates a 28–38% reduction in canopy-top g_s under elevated C_a relative to current concentration conditions. This range encompasses an average midday reduction of 34% for g_s of canopy-top maize leaves as observed at SoyFACE in 2004 [Leakey *et al.*, 2006b].

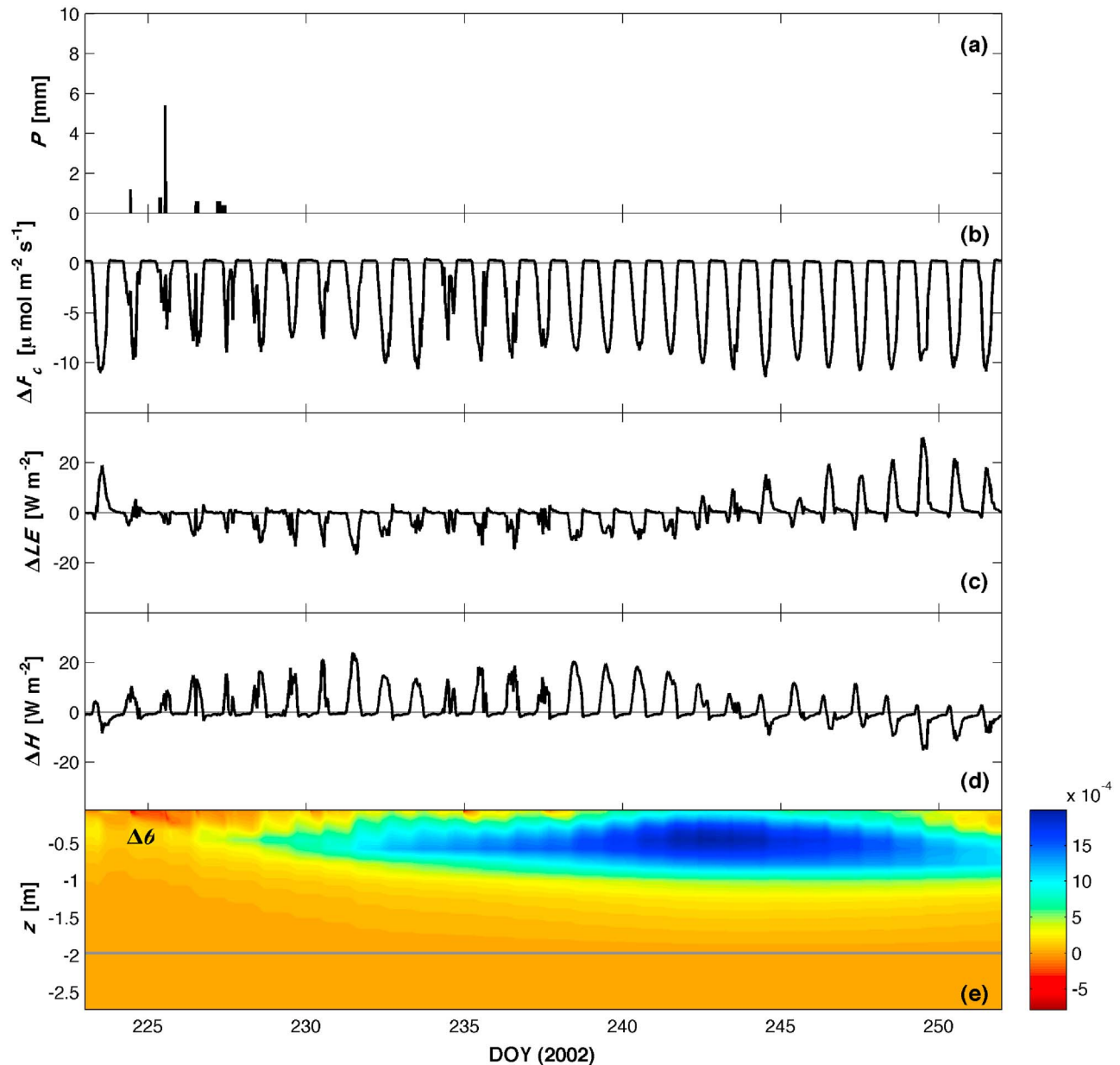


Figure 10. Several week period in 2002 depicting the impact of soil moisture conservation under elevated C_a on energy partitioning of the soybean canopy. (a) Precipitation over this period. Figures 10b–10d present the differences (elevated C_a – current C_a cases) in (b) CO₂, (c) latent, and (d) sensible heat fluxes. (e) The difference in soil moisture through the modeled soil profile, with a gray line indicating the depth of the root zone.

moisture stress during the 2002 study season. This reduction in ΔLE is also seen as θ_{wgt} is reduced for both crops. The change in LE for soybean flattens as R_g rises due to the offsetting influences of the direct stimulation of elevated C_a on A_n resulting in increased g_s and the ecophysiological response of elevated CO₂ on stomatal aperture.

[45] The changes in H mimic those of LE for both crops, but are opposite in sign, as energy partitioned to LE under current climate conditions is allocated to sensible heating by the warmer canopies under elevated C_a . The magnitude of the increases in H is less than the magnitude of the decreases in LE for maize, as the increased T_l forces more energy to be dissipated as emitted longwave under elevated C_a . However,

this is not the case for soybean as structural acclimation allows for the capture of more radiation which is dissipated primarily as H .

3.7. Impact on Moisture Stress

[46] As an example of the impact of elevated C_a on stomatal closure and the conservation of soil moisture through the shifted energy partitioning from LE to H mentioned above, Figure 10 presents the changes in F_c , LE and H for the soybean canopy over a several week dry period in 2002. A conservation and buildup of soil moisture under elevated C_a over the initial two weeks following a rain event, relative to the soil moisture state under current CO₂ conditions, is

seen in Figure 10e. Over this period, the changes in energy flux partitioning result in an increase in the Bowen Ratio (H/LE) due to ecophysiological adjustment. As the dry period continues, the canopy experiencing current C_a begins to experience water stress. The canopy experiencing elevated C_a is able to utilize the conserved soil moisture to continue to transpire at potential rates, causing a reversal in typical patterns of ΔLE and ΔH . In Figure 10b, a further increase in the uptake of CO₂ for the vegetation in elevated C_a can be seen at the time the current C_a vegetation begins to become water stressed. The negative values in ΔF_c for the C3 soybean are generally due to CO₂ fertilization, but this increase relative to current CO₂ vegetation demonstrates how mitigation of drought by way of ecophysiological acclimation can further augment vegetation CO₂ uptake, and potentially crop productivity.

3.8. Variation of Canopy-Atmosphere Exchange at Different Magnitudes of Elevated C_a

[47] The SoyFACE experimental facility applies an elevated CO₂ concentration of 550 [ppm], as this is projected to be the global mean concentration by 2050 [Houghton et al., 2001]. A benefit of a numerical model that has been demonstrated to accurately capture observed canopy responses under environmental change is the ability to synthetically explore a range of possible scenarios that extend beyond the feasibility of current observational methods. In order to examine how the canopy-atmosphere fluxes of CO₂, latent and sensible heat would be altered across a broad range of ambient CO₂ concentrations, we ran simulations for both crops with ambient CO₂ concentrations ranging from 400 to 700 [ppm], representing expected near-term changes out through the end of the current century [Houghton et al., 2001]. For soybean, structural and biochemical acclimation are both considered. The trends in the magnitudes of these acclimations are uncertain as FACE experiments have only been performed with elevated C_a of 550 [ppm]. We ran two scenarios for soybean, with the first scenario assuming that the percent changes in LAI and down-regulation remain constant at the values observed at 550 [ppm] for the range of C_a examined here. The second scenario assumes a linear trend from no change at current C_a to the observed changes at 550 [ppm], extrapolating the linear trends to the concentration values greater than 550 [ppm] examined here. All study years were used in this analysis except for 2002 in order to eliminate the effects of significant water stress. The percent changes in accumulated total daytime ($R_g > 10$ [W m⁻²]) flux (Δf), relative to the flux at current C_a (370 [ppm]), are calculated as

$$\Delta f = \frac{\sum_{i=1}^n f_{elev,i} - \sum_{i=1}^n f_{curr,i}}{\sum_{i=1}^n f_{curr,i}} * 100$$

where $f_{elev,i}$ and $f_{curr,i}$ are the fluxes under elevated and current C_a during the i th time period, respectively.

[48] The mean change in daytime A_n for soybean is seen to increase from a few percent at 400 [ppm] to almost 40% at 700 [ppm] (Figure 11a). The increase falls further from a linear rise (presented as dotted lines) with rising elevated

concentrations, as the nonlinear response of A to C_i saturates with increasing concentrations. The constant and linear trend scenarios produce almost identical changes in A_n across the range of concentrations due to the insensitivity of ΔA_n to structural and biochemical acclimation (see Figure 5). Maize canopy A_n shows no stimulation over the elevated CO₂ range.

[49] $LE(H)$ of maize falls (rises) as a nonlinear function of elevated C_a (Figures 11b and 11c). The reduction in the rate of decrease (increase) is due to the nonlinear dependence of g_s on C_s , the leaf surface CO₂ concentration that is controlled by C_a . Despite the slight nonlinearity in the trends in changes in energy partitioning, the mean daytime Bowen Ratio continues to increase through 700 [ppm] from the large changes in energy partitioning estimated for 550 [ppm] (see Figure 6). These modifications will likely have a significant influence on boundary layer development. Particularly high percentage increases in H are predicted as C_a increases due to the relatively small proportion of energy partitioned to H under current C_a .

[50] For soybean, LE under constant acclimation shows an increase at 400 [ppm] as the increase in A_n is able to offset the ecophysiological response to the small concentration increase, by way of the linear dependence of g_s on A_n . The rate of decrease (increase) of $LE(H)$ is less than that of maize, as the direct stimulation of C3 photosynthesis partially mitigates some of the reduction in g_s as ambient C_a rises. The linear acclimation scenario demonstrates a similar effect seen in Figure 5, with a 2% increase in ΔLE and 10% increase in ΔH at 700 [ppm]. Given the magnitudes of the changes for the constant acclimation case, the modifications assuming linear trends in structural and biochemical acclimation are minor.

[51] The change in mean water use efficiency (WUE), defined here as the total daytime A_n divided by total daytime LE , is seen to increase for both crops through the entire range of C_a (Figure 11d). Maize WUE increases from more efficient water use due to ecophysiological adjustment that results in decreasing LE with elevated C_a . The reduction in LE for soybean is not as great as that of maize, but large increases in A_n stimulated by elevated C_a result in greater increases in WUE relative to those of maize. The increased WUE under projected future conditions indicates a capability of both crops to remain resilient under potential future increases in frequency of climatic extreme events such as drought [Trenberth et al., 1988; Rosenzweig et al., 2001].

4. Conclusions

[52] Free Air Carbon Enrichment (FACE) observations [Lewin et al., 1994; Miglietta et al., 2001] have produced a wealth of knowledge about how vegetation properties and functioning are modified in open-air, CO₂ enriched environments. While circumventing many of the problems associated with enclosure systems [Arp, 1991; Sage, 1994; Long et al., 2006], observations are spatially localized with respect to position in the canopy [Ainsworth and Long, 2005] and temporally localized with respect to sampling dates, leaving open questions as to how observed leaf-level changes scale to canopy-level responses across varying environmental conditions. In this paper we applied a multi-layer canopy-root-soil system process model (MLCan),

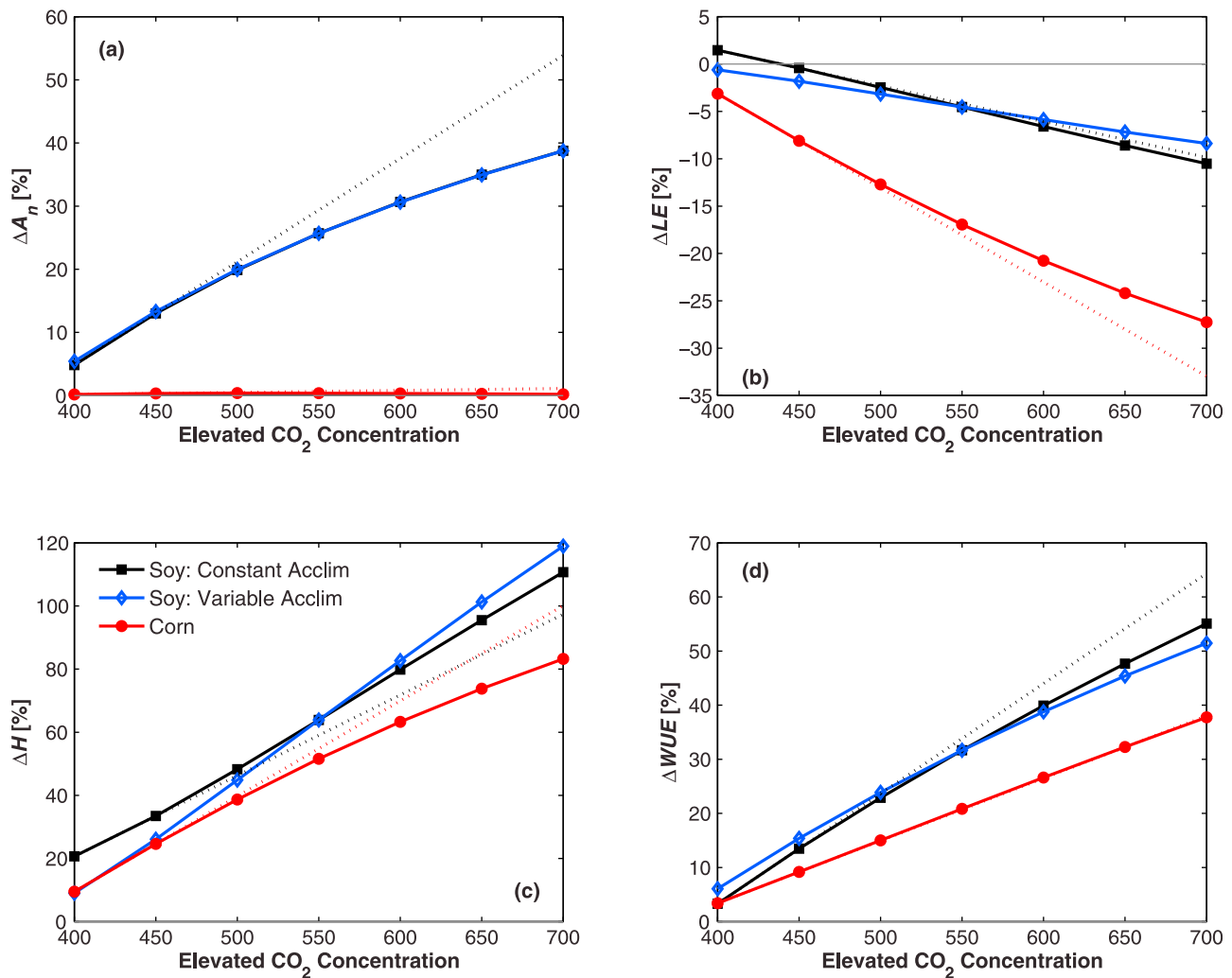


Figure 11. Examination of the modification of mean daytime canopy-atmosphere exchange at several levels of elevated C_a . The mean daytime ($R_g > 10$ [W m^{-2}]) percent change in net (a) carbon dioxide, (b) latent heat, and (c) sensible heat fluxes, and (d) WUE . Estimates for soybean, assuming structural and biochemical acclimation is constant for all elevated C_a , are given as black squares/lines. Estimates for soybean, assuming a linear trend in the magnitude of structural and biochemical acclimation, are presented as blue squares/lines. Estimates for maize are given as red circles/lines. Dotted lines represent the linear trend in percentage flux change from the first two elevated CO₂ concentrations (400 and 450 [ppm]).

previously validated for several seasons of eddy covariance data [Drewry *et al.*, 2010], to the examination of the within-canopy and canopy-integrated responses of central U.S. maize (C4) and soybean (C3) to elevated CO₂ concentrations projected for the next several decades.

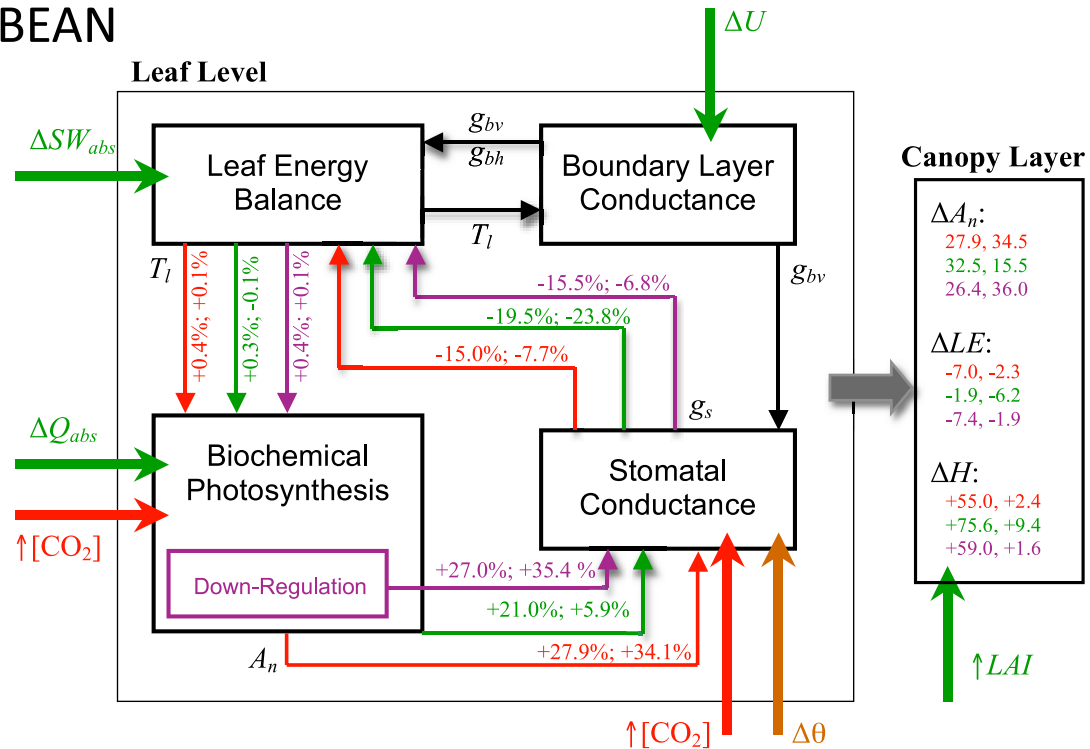
[53] Observations from SoyFACE provided data for leaf-level validation and specification of the magnitudes of structural augmentation and photosynthetic down-regulation. Through the incorporation of observed structural and biochemical plant acclimation, and accounting for the widely

Figure 12. Schematic depicting changes in coupled leaf-level processes for (top) soybean and (bottom) maize due to the different acclimatory responses of each crop. Modeled percent changes in leaf-level A_n , T_l , and g_s are indicated on each arrow: the left number refers to the percent change at $z/h = 0.85$, the location of the upper canopy maximum in soybean LAD, and the right number refers to the percent change at $z/h = 0.45$, the position of a lower canopy maximum in soybean LAD [see Drewry *et al.*, 2010, Figure 2]. Large arrows indicate modifications to system forcings: red refers to the effect of elevated C_a as a stimulant of C3 photosynthesis and its direct effects on stomatal aperture; green augments the red scenario with the effects of changes in canopy structure that result in modified radiation forcing, wind speed, and environmental gradients through the canopy; purple augments the red scenario with observed down-regulation of leaf-level photosynthetic capacity; and brown indicates an effect of soil moisture conservation due to stomatal closure over longer timescales. Only the effects of ecophysiological adjustment to elevated C_a , and the resultant soil moisture conservation, are represented for maize. Percent changes in net fluxes for the entire canopy layers are presented in the boxes on the right side.

observed ecophysiological reduction of stomatal conductance under elevated CO₂, a set of MLCan simulations were conducted to untangle the roles of each observed acclimation in vegetation responses. Figure 12, which augments Figure 2 of Drewry *et al.* [2010], presents the mean midday (10AM to 2PM) changes in leaf states and layer fluxes at two vertical positions over the three simulated seasons for each crop.

[54] Contrasting the effects of ecophysiological acclimation alone (red arrows in Figure 12) with the additional affects of structural acclimation (green arrows in Figure 12), the stimulation of soybean photosynthesis by elevated CO₂ partially offset the reduction of stomatal conductance. As shading reduced the incident *PAR* flux on the foliage, A_n per unit leaf area was reduced with a consequent increase in the

SOYBEAN (C3)



MAIZE (C4)

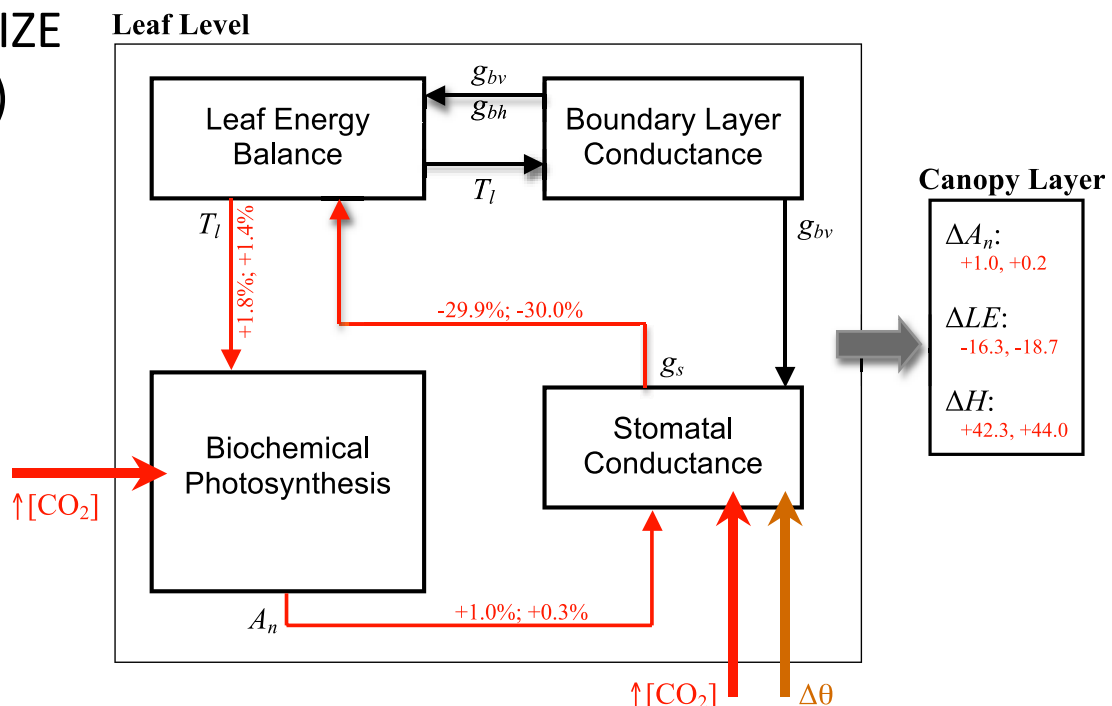


Figure 12

reduction of g_s . At the canopy scale, across nonwater stressed periods, ecophysiological acclimation and CO₂ fertilization accounted for a diurnal mean 34% increase in CO₂ uptake and only a 7% reduction in transpiration for soybean. Somewhat counterintuitively, the additional leaf area from structural acclimation resulted in a reduction of the increase in net CO₂ uptake to 30% due to greater respiration losses over the diurnal period. Greater shortwave radiation absorption was concentrated in the dense upper canopy (see Figure 1), where foliage was light saturated, further shading foliage below that could have more efficiently utilized additional PAR. An average increase in shortwave absorption of approximately 15 [W m⁻²] at noon (Figure 1) resulted in a negligible increase in canopy-integrated CO₂ uptake (Figure 5), pointing to a future inefficiency in canopy architecture of this crop.

[55] Biochemical down-regulation (purple arrows in Figure 12) had a negligible effect on leaf-level and canopy-integrated (Figure 5) photosynthesis. Leaves operating at a higher C_i (Figure 4) experience a shift in photosynthetic control from Rubisco to RuBP regeneration limited [Bernacchi et al., 2005a], with these results found here supporting a hypothetical optimality in the possible reallocation of photosynthetic resources away from Rubisco.

[56] Maize (C4) leaves, which only experienced ecophysiological acclimation and by contrast showed negligible stimulation of photosynthesis under elevated CO₂ (Figure 12, bottom), had leaf-level reductions in stomatal conductance approximately two and four times greater for the upper and middle canopy leaves relative to soybean, respectively. At the canopy scale the maize crop exhibited a mean diurnal decrease in transpiration of 19%, several times greater than the 4.5% decrease of the soy crop when all observed acclimations were incorporated into MLCan.

[57] As sensible heat fluxes are generally much lower for these crop systems (mean noon Bowen ratio of 5.4 for soybean and 3.1 for maize calculated from eddy covariance observations), mean diurnal increases in sensible heat release to the atmosphere under elevated CO₂ were large: 22% for soybean and 48% for maize. These large shifts in surface energy dissipation from transpiration to sensible heating have implications for land-atmosphere interactions at regional scales, where daytime atmospheric boundary layer (ABL) growth, temperature and moisture concentrations are strongly coupled to land surface functioning. At larger scales, the coupling of the land surface to the ABL introduces multiple feedback pathways [McNaughton and Spriggs, 1986; Jarvis and McNaughton, 1986; Jacobs and de Bruin, 1997] that can modify the magnitude of the stomatal response to climate changes [Jacobs and de Bruin, 1997; Wilson et al., 1999]. Future work will address the issue of regional-scale responses of the central U.S. agro-ecosystem to potential future climate change (D. T. Drewry et al., manuscript in preparation, 2010), including the magnitude and direction of the vegetation-ABL feedback and dependencies on synoptic-scale meteorological conditions.

[58] **Acknowledgments.** This research is primarily funded by NSF grant ATM 06-28687 and partially supported by NOAA grant NA 06-OAR4310053. We wish to thank the PIs of the Bondville Fluxnet tower and the FACE experimental facility. Benjamin Burroughs conducted valuable data synthesis work that is gratefully acknowledged. Insightful comments of Lisa Ainsworth and Andrew Leakey helped shape some initial thinking on this project.

Juan Quijano, Venkat Srinivasan, and Phong Le provided valuable comments on early versions of the manuscript. We also thank the Editor (Dennis Baldocchi) and an Associate Editor for *JGR-Biogeosciences*, along with two anonymous reviewers, whose insightful comments greatly improved the manuscript.

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